# FUNCTIONAL TRAITS COMPLICATE THE PICTURE OF TEMPORAL BIODIVERSITY CHANGE IN BIRD AND MAMMAL COMMUNITIES

#### A Preprint

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## Abstract

Aim: Despite unprecedented environmental change due to anthropogenic pressure, recent work has found increasing dissimilarity due to turnover but no overall trend in species diversity through time at the local scale. Functional diversity provides a potentially powerful alternative approach for understanding community composition by linking shifts in species identity to mechanisms of ecosystem processes. Here we present the first multi-taxa, multi-system analysis of functional change through time.

7 Location: Global, with a North American focus

Time period: 1923-2014

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9 Major taxa studied: Mammals, Birds

Methods: We paired thousands of bird and mammal assemblage time series from the BioTIME database with existing trait data representative of a species' functional role to reconstruct time series of functional diversity metrics. Using generalized linear mixed models, we estimated general trends in those metrics and trends for individual studies.

Results: We found no overall trend in any functional diversity metric, which held even after correcting for changes in species richness. At the study-level, there was substantial heterogeneity in the direction and type of functional change exhibited. None of the included study characteristics such as taxa, realm, biome, or protection status were significantly related to the type of change exhibited by a community.

Main Conclusions: General trends indicate that on the aggregate one type of functional shift is not more prevalant than the other across many taxa, biomes, and realms. At the study-level, the majority group of studies showed no species or functional trends, but other types of change were manifest for multiple studies, including studies experiencing changes in functional redundancy, increased species and functional richness, or loss of functional richness. With no one prevailing scenario of change, it will be critical to link change scenarios to ecological context.

 $\boldsymbol{Keywords}$  biodiversity change  $\cdot$  functional traits  $\cdot$  global change  $\cdot$  time series

# 1 Introduction

Ecological communities are experiencing unprecedented change as a result of anthropogenic pressures such as climate change, land use change, and invasive species. Impacts of these pressures are well documented at a global scale by an accelerating global extinction rate (1), and fundamental changes in some of the most well-studied systems (e.g. coral bleaching, 2). At the local scale however, species diversity tells a different story. Recent syntheses of local trends in biodiversity over time have found no net change in local species diversity despite ongoing turnover (3–6) and evidence of significant shifts in community composition

underlying consistent species richness (7–9). While communities are clearly changing, our most common 34 species-based approaches do not fully capture the nature of that change. 35

Using general trends derived from limited data as a diagnostic for the state of biodiversity or directing 36 conservation is a topic of ongoing debate. Global analyses have been heavily criticized for geographic biases, 37 lack of data in the most heavily impacted areas, and exclusion of individual studies' ecological context (10–12). Many of these criticisms reflect limitations of ecological data on the whole, leading to a call for additional 39 data not only to fill geographic and temporal gaps, but to flesh out key characteristics of communities (13, 40 41

Functional diversity offers a potentially powerful addition to species-based approaches for detecting and 42 describing community change by providing a mechanistic link between species' response to environmental 43 change (response traits) and the processes they perform (effect traits) (15–17). By describing the functional trait space, functional diversity metrics capture the disproportionate impact of losses or gains of functionally 45 unique species. Functional diversity metrics may therefore illuminate joint responses from functionally similar 46 species or communities undetectible by looking at species identity alone. 47

The expectation for functional change across communities is not obvious from past work, and may or may not follow taxonomic trends (13). While loss of functional diversity is frequently cited as one of the most pressing concerns of the anthropocene (18-20), functional diversity may be maintained even when species are lost from a community (21, 22). Forecasts of functional loss range from negligible (23) to dire (24, 25). And while some observed trends show significant functional loss (26) others document no loss even in some of the most heavily impacted communities (27–29). On paleoecological time scales, the functional space shows mixed responses to environmental change and extinction events (30, 31), with significant impacts of species extinctions on functional diversity in some taxa and not others (32). For some time periods, functional diversity appears to be maintained for substantial portions of geological time (33). Contemporary, broad-scale examinations of functional change are limited to only a few taxa-focused studies, but show for example functional richness increases for both North American birds [@barnagaud2017; @jarzyna2016] and ray-finned fishes, sharks, and rays (34). Additionally, these taxa have been the subject of substantial conservation investment and policy action, so are not necessarily representative of trends for other taxa or the same taxa in different locations.

Here we leverage ongoing efforts to assemble functional trait data and recent computational advances to perform the first multi-taxa, multi-realm assessment of functional diversity change through time. We focus on mammal and bird species as a subset of the world's biodiversity of particular conservation concern that is heavily impacted by anthropogenic change. While examining trends in plants, invertebrates, and other vertebrate species is of equal interest, trait data for those taxa raise additional challenges such as limited and biased species coverage (35), a lack of accepted species-level means, and differences in the types of traits collected. To ensure comparability across taxa in trait type and data quality we therefore focus on mammals and birds. We include body mass, foraging and dietary traits that were intentionally selected to be representative of a species' Eltonian niche, thereby summarizing the functional role they play in the community (36). An initial assessment of amphibian trends is included in the supplement, but excluded from general trend assessment here due to limited geographic coverage.

We assess thousands of mammal and bird functional diversity time series to determine whether or not the addition of functional trait data gives a clarifying picture of biodiversity change across communities. Rather 73 than testing specific hypotheses of change we present a few areas of change consensus across communities, and even more scenarios where the relationship between functional and species change are unexplained and warrant further theoretical and experimental examination. We present results at three different levels: general 76 trends across communities, trends for communities with similar characteristics (taxa, biome, realm, protection status), and trends for individual studies.

#### Material and Methods $\mathbf{2}$

#### 2.1Data 80

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We obtained mammal and bird time series from the BioTIME database, a global repository of high-quality 81 assemblage time series collected from the literature and ongoing monitoring efforts. Data is structured such 82 that a study encompass all data collected following consistent sampling protocols and may contain multiple 83 time series from separate locations. Time series represent full assemblages rather than populations of 84 single species (31), and all time series include abundance of observed species. Following best practices for 85 the database (37), studies with multiple sample locations were split into individual time series following a standardized spatial scale. Scale was set by a global grid with cell size determined based on the sample extent of studies with only a single location (see 31 for details on how sample extents were defined), with the area of each cell set to one standard deviation away from the mean of the single extent locations. All samples from a study within a single cell were considered to be a single time series, and species abundances were combined for all samples.

We used trait data from the Elton Trait Database, which consists of species-level means for traits that represent species' multifaceted role in the community (36). Traits include: body mass, diet, active diel period, nocturnality, forest foraging strata, pelagic use. Multiple traits (i.e. diet, foraging strata, activity seasonality, active diel period) were broken down into percentage or binary use for each level.

In order to ensure taxonomic consistency across datasets, BioTIME species were paired with trait data based on their species identifier from the Integrated Taxonomic Information System database (retrieved 09-15-2020 from the on-line database, https://doi.org/10.5066/F7KH0KBK), obtained through the taxadb R package (38, 39). If more than one species in the assemblage data resolved to the same identifier, observations were considered the same species. For trait data, traits for all species of the same identifier were averaged. Only studies for which at least 75% of species had trait data were included. In order to have a sufficient number of species to calculate functional diversity metrics, years with fewer than 5 species observed were also excluded. Sensitivity analyses were conducted for the trait coverage threshold and the duration of included time series.

Many studies had a variable number of samples within years. To account for this inconsistency in sampling effort we used sample-based rarefaction by bootstrap resampling within years for each time series based on the smallest number of samples in a year for that time series.

Our final dataset included 2,432 time series from 50 studies in 21 countries and 12 biomes and 6 different 107 traits (Fig 1). Data came from both terrestrial and marine realms and five biomes (Global, Polar/Temperate, 108 Temperate, Temperate/Tropical, Tropical). The earliest sample was in 1923 and the most recent was in 2014. 109 While it is not possible with this data to directly assess the level of human impact occurring for each study, 110 we include binary protection status as a coarse indicator of impact level. However, protected areas were 111 almost exclusively from temperate terrestrial studies (with one tropical study), so results are confounded 112 by multiple other study characteristics. For a full breakdown of studies and their characteristics, see the 113 supplement. Our final dataset reflects many of the data biases that make global synthesis work challenging, 114 including geographic bias, a bias away from areas currently under the greatest threat, and a bias towards 115 shorter time series. We address these shortcomings and their potential impact on our results in the discussion. 116

# 2.2 Diversity Metrics

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We calculated yearly metrics of functional and species diversity for each time series. Species-based metrics include species richness (S) and Jaccard similarity (J) as a measure of turnover. Jaccard similarity was calculated relative to the first observed year for a time series. A negative trend in J would therefore indicate decreasing similarity. We did not impose a correction for unobserved species as non-parametric estimators do not assign species identities to corrected richness values, and therefore could not be propagated to the functional diversity metrics.

Functional diversity metrics were calculated using the dbFD function from the FD R package (40). Here 124 we report functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv) which 125 together describe three complementary characteristics of the functional space (41, 42). FRic assesses the volume of the trait space occupied by species in the community, with higher values indicating communities 127 with species of more extreme trait values. FEve describes how species are distributed across the trait space 128 and how abundance is distributed across species. Higher values of FEve indicate more even spacing of 129 species in the trait space and individuals across species. FDiv measures the degree to which species and 130 their abundances maximize differences in the functional space. Higher values of FDiv therefore correspond to 131 communities where many highly abundant species are on the edges of the trait space. We also calculated 132 the community-weighted mean (CWM) of included traits to examine shifts in the distribution of each trait. Hereafter we refer to results for functional diversity metrics (FRic, FEve, FDiv) and composition metrics 134 (trait CWM's). 135

All available trait data for each study were included in functional diversity calculations with the exception of traits that were the same value for all observed species in the study. For variables with multiple levels each level was included as a separate trait axis. Continuous traits were z-score scaled to give each trait equal weight in the trait space (43, 44). Before calculating diversity metrics, dbFD reduces the dimensionality of the trait space by performing PCoA. We limited the number of included PCoA axes to the maximum number

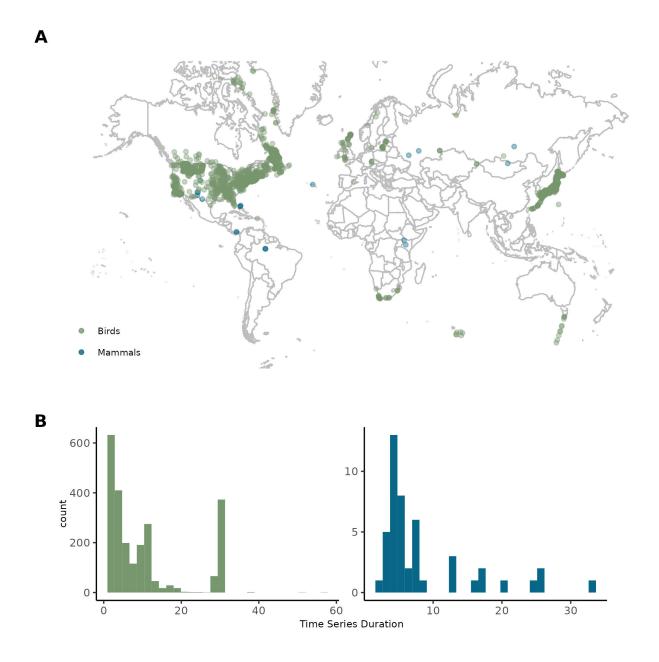


Figure 1: A) Map of time series locations with points colored by taxa, and B) histograms of time series duration broken down by taxa.

of traits that fulfills the criteria  $s >= 2^t$ , where s is the number of species and t is the number of traits. This restriction allows for enough axes to capture the trait space while maintaining computational feasibility (45). Metrics incorporated weighting based on species abundance.

# 44 2.3 Null Models

To assess functional change independent of species richness we calculated the standardized effect size (SES) for each of the three functional diversity metrics (FRic, FEve, FDiv) from null estimates (46). Null model corrections allow us to assess the degree to which the observed functional diversity metric deviates from the value expected by chance in a randomly assembled community. Null estimates were calculated for each rarefied sample by randomly sampling species from the species pool for each year and randomly assigning observed abundances to species. 'Species pools were unique for each time series and included all species observed over the course of sampling, therefore accounting for geographic restrictions in species availability. This process was repeated 500 times to get an estimate and standard deviation of the null expectation for the metric for each rarefaction sample for that time series. We used these values to calculate SES using the following formula:  $SES = [F_{obs} - mean_{(F_{null})}]/SD_{(F_{null})}$ . We then calculated the median SES estimate for each metric from all the rarefaction samples for a time series. SES estimates can be interpreted as how much of the functional characteristic (richness, evenness, divergence) was observed beyond what was expected by chance for a community of that species richness. This approach will be less accurate for shorter time series, as we likley will not have captured all available species in the true species pool, but it is impossible to know whether the mean estimate from the null model is an over or under estimate without knowing the functional characteristics of the missing species.

# 2.4 Analysis

We estimated general trends across bird and mammals communities for each diversity metric using a linear mixed effects model with a random slope and intercept for each study and each time series nested within the study, methods which deal well with the inherent imbalances in our data. We fit 18 individual CWM models, one for each trait included in the analysis. All time series with data for a given trait were included in the corresponding CWM model. We estimated study level trends using individual linear models. For studies with more than one times series we fit a random slope and intercept for time series. Some study-level models could not be fit for five studies for at least one metric due to data limitations, but those studies were still included in the general models. They represented 12 of 1350 study-level models fit for each metric. For further details see the supplement. Where appropriate, response variables were log or log(x+1) transformed to better fit model assumptions of residual normality.

To test for trends within and between different levels of taxa, biome, realm, and protection status we fit separate models with each of those factors added as a predictor interacting with time to the original model structure. We estimated within-level slopes and calculated between-level contrasts using the *emmeans* package (v1.8.2, 47). For some levels of the categorical variables we did not have a sufficient number of studies to estimate a general trend, we therefore refrained from interpreting results for levels where there were fewer than three studies. We assessed the impact of time series duration and start year on study-level trends using linear models with duration and start year as predictors. All models in our analysis were fit using the lme4 (v1.1-30) package in R (v4.2.3) and p-values were calculated by Satterthwaite's degrees of freedom method using the lmeTest (v3.1-3) package with a significance level of  $\alpha = 0.05$  (48–50).

# 3 Results

We found no significant overall temporal trend in species richness or functional diversity metrics including functional richness, evenness, or divergence (observed or corrected) (Fig 2). We did find a significant overall decrease in Jaccard similarity, indicating accumulating changes in species composition. Non-significant overall temporal trends indicate that although some studies experience increasing or decreasing trends, the average trend across studies was not significantly different from zero' (Table ??). Within-group trends for different taxa, biomes, realms, or protection statuses were also non-significant for richness and functional diversity metrics, with the exception of a significantly increasing trend for functional evenness of marine studies, and a significantly decreasing functional richness slope for mammal studies. However, trends were not exhibited for the corrected metric indicating that differences in functional diversity metrics were largely due to changes in species richness. The general trends for CWM models were similarly not significant, with a significant positive trend for only percentage of fish in diet composition.

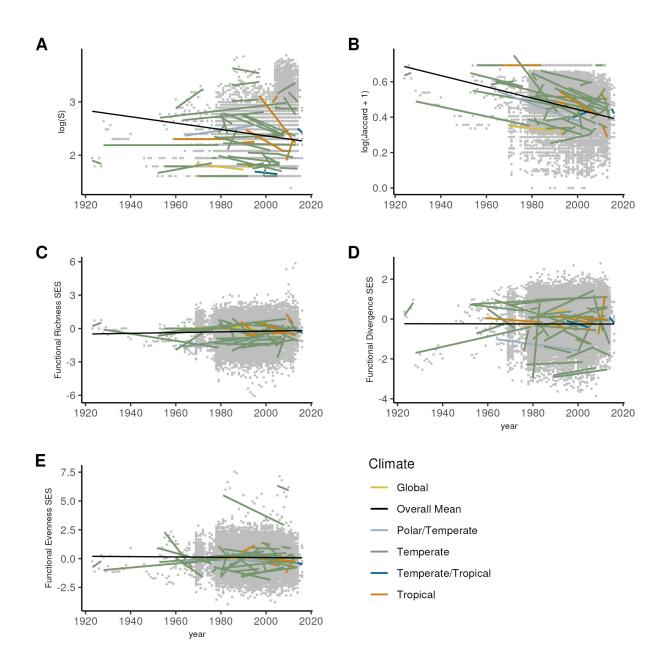


Figure 2: Plots of time series-level trends with line color corresponding to climatic region, with data points in grey and the overall mean slope for a metric in black for A) log species richness, B) Jaccard similarity, C) Functional Richness SES, D) Functional Divergence SES, and E) Functional Evenness SES

We did find significant differences between taxa, realms, and biomes for Jaccard similarity and some of the CWM's. For example, while Jaccard similarity was decreasing in the general trend and there were significant within group slopes for Mammals, Birds, Terrestrial, Temperate, and Tropical communities, there was no significant slope for the marine realm, indicating that the general trend is mostly driven by turnover in terrestrial communities. We also found a significant decrease in Jaccard similarity in unprotected areas only, with no trend for protected areas. We found significant dietary shifts across communities, with a significant general trend of increasing fish consumption, which was also reflected in increasing fish consumption trends for Bird studies and Temperate studies. We found a significantly increasing trend in nectar consumption for Temperate studies but a significantly decreasing tend for Tropical studies. We found significantly decreasing trend for vertebrate consumption in Marine studies and Tropical studies.

At the study level, 16 of 50 studies exhibited a significant trend in species richness and 11 exhibited significant turnover. For uncorrected functional diversity metrics, 25 of 50 studies exhibited a trend in a least one metric, and 15 of 50 studies exhibited a significant trend for at least one corrected metric (Table ??). In general, there were more significant trends for uncorrected metrics, with some disappearing after correction, indicating that those trends were likely due to changes in the number of species. Hypothesis testing for study-level trends is likely affected by multiple testing issues and some trends identified as significant are therefore potentially spurious. Rather than interpreting changes in specific studies, we present these results as a general picture of the kinds of trends experienced by communities. 

Study-level slopes were significantly related to start year of the time series for Jaccard similarity and functional evenness models, both of which had significantly more negative slopes with more recent start year. No functional diversity metrics were significantly related to the duration of the time series.

We assessed the sensitivity of general trend results to major data processing decision by rerunning models with increasingly conservative subsets of the data. Trends for Jaccard similarity and fish consumption were not sensitive to either time series duration or trait coverage. After excluding time series with less than three years we found an increasing trend for body mass that remained after excluding time series of less than four and five years. We also found a decreasing trend in functional richness for models with a minimum of three years and a minimum of five years. A decreasing functional richness trend was found for models with a min of 85% trait coverage, but not the other two coverage levels. A complete list of models run in the sensitivity analysis and their results can be found in the supplement.

# 222 4 Discussion

Our study represents the largest broad-scale multi-taxa assessment of functional change through time to date, giving a first look at aggregate and local trends in functional diversity in mammal and bird communities. Our results show that the addition of functional traits illuminates a few consistent functional trends across communities, but largely complicates rather that clarifies the story of biodiversity change. While the characteristics of species clearly matter, instead of unifying the nature of communities' change, they more often distinguish them. In general, we found a few areas of consensus for models where communities were aggregated (general trends, trends by taxa, biome, realm, protection status), and vast heterogeneity for study-level models.

### 4.0.1 Evidence of consensus

The most stark area of consensus was the lack of general trend aggregating across communities. We did not detect an overall trend in any functional diversity metric, corrected or uncorrected. As with previous species-based syntheses, we also found no overall trend in species richness accompanied by increasing dissimilarity through time (31), indicating that non-significant trends in functional metrics are consistent with similar well-documented species derived trends. We found significant turnover for all biomes, realm, and taxa except for marine studies, which stands in contrast to other global estimates of biodiversity change that found higher turnover in marine systems than terrestrial (37). However, previous global estimates are dominated by fish communities which we exclude here and may be driving the overall trend while disguising relative stasis in marine bird and mammal communities.

We found evidence of functional richness loss in mammal studies, with a loss trend significantly different from zero and significantly different from the trend for birds, indicating a potential loss of functional capacity in these communities. This result is consistent with previous work linking anthropogenic drivers such as habitat loss, poaching, and human modification and development to loss of functional diversity in mammal communities across the globe (51–53). However we did not find trends outside the random expectation for

species loss, in contrast to expectations for multiple continents based on IUCN risk categories (51). In general, functional capacity of mammals shows greater declines that bird communities.

We also found evidence of increasing evenness for Marine studies. The empirical link between changes in evenness and ecosystem process is the most poorly studied of the metrics, however theory indicates that increased evenness improves function and stability (54). If one or a few species become largely dominant in a community, function will be the result of only those species rather than spread out across a wealth of species responding independently to environmental change (42, 55). Further, there is some evidence that maintaining evenness is important for supporting multifunctionality in communities (56). The majority of marine studies are of seabird communities (7 of 9), so the general trend may be an early indicator of pay off from investments in sea bird recovery, which is also indicated in recent species-based work (57).

Compositional shifts shown by significant trends in CWM's were restricted to dietary traits, with no evidence of a trend in foraging traits or body mass. Increases in fish consumption for bird and temperate studies my be the product of increased availability of easy fish from commercial fishing operations as fish are processed or stocking of inland waterways for sport fishing. However, fisheries also have negative impacts on waterbirds through competition for fish or bird mortality due to by catch. Decreases in nectar consumption for tropical studies is likely due declines in bat species, as 4 of the 5 tropical studies are for mammal and bats were the only nectar consuming mammals sampled in our data. Interpretation of the increases for temperate studies is less clear, as temperate studies included many bird communities with a variety of nectar consumers. Similarly, decreasing trends for vertebrate consumption in marine and tropical studies are not obviously consistent with known changes in those contexts and warrant further examination.

# 4.0.2 Study heterogeneity

 At the study-level, our results run contrary to our hope for a clearer picture of biodiversity change through a functional lens. The lack of general trend in functional diversity metrics belies a huge range of positive and negative trends at the study-level. In order to simplify discussion, we will talk about the implications for ecosystem process and vulnerability for communities grouped by their concurrent change in corrected functional diversity metrics, species richness and turnover split into positive, negative or no trend. While there are over 150 possible combinations of change direction (or no change) in the 5 metrics, we discuss here the six scenarios that occurred in more than one study: no change, species loss or gain only, loss of functional evenness, species richness loss with species turnover, and increase in species and functional richness accompanied by significant turnover. We focus on these scenarios to combat potential spurious results due to multiple testing, as it is unlikely all observations of the same scenario are due to false positives. We include a break down of the number of studies in each scenario to illustrate relative number of studies in each group, but emphasize that the absolute number is likely impacted by multiple testing.

The majority group of studies exhibited no trend in any species or functional diversity metric. Contrary to the expectation due to anthropogenic and global change stressors, these communities do not show significant changes over the course of the observation window. Studies in this group span the distribution of study durations excluding only the very longest running studies, with the longest no change time series lasting 23 years. They also included both bird and mammal studies and only four were located in protected areas, indicating that the lack of trend is not restricted to a specific ecological context or those communities most insulated from human impact.

The lack of trend could be the result of multiple possible scenarios. First, these may be communities resisting perturbations or simply not experiencing significant perturbations. Given the studies in this group come from all possible taxa, realms, biomes, and protection statuses, evidence points to communities resisting perturbation, offering some hope that there are areas of the globe where communities are fairing well for now. Alternatively, these may be communities that have experienced or continue to experience significant stress, but lost species or functional diversity outside the observation window. This could be true particularly for North American mammal communities where trophic downgrading and megafaunal losses occurred hundreds of years ago [citation]. Third, these communities may be experiencing directional shifts undetectable by available data. For example, species-level trait data does not capture intraspecific shifts in the trait space, which can represent significant changes in the functional space as a whole and impact maintenance of ecological 

Three of the groups fit under the broad umbrella of changes in redundancy. By definition, if a community gains or loses species while functional metrics are unchanged, those species represent an increase or decrease in redundancy, so we include communities exhibiting gains or losses in species richness with no change in functional metrics or turnover and species richness loss with significant turnover in this umbrella. For

communities exhibiting loss of redundancy (declining species richness), ecological processes are likely being maintained, but capacity to respond to future stressors is reduced (58). These communities are actually fairing better than expected looking at species-based metrics alone, but are also in a precarious position for maintaining ecological function into the future (59). Conversely, communities exhibiting a increase in redundancy (via an increase in species richness) are becoming better positioned to respond to future stressors, but are not actually expanding their functional capacity as may be assumed by looking at species gains alone (60).

The next group of studies exhibit an increase in species richness and functional richness with significant 308 turnover. While these communities are losing some species that are functionally redundant or functional 309 analogs of species additions, they are gaining even more species that expand the functional space. These 310 communities have a hopeful trajectory, as they are improving their functional capacity and potentially their 311 functional redundancy, likely leading to robust future ecological function. Notably, the studies that exhibited 312 species richness increases (in this group with increasing functional richness, as well as communities without 313 functional richness increases) were exclusively from terrestrial, temperate (sometimes temperate/polar) bird 314 communities and occurred in countries where there has been a significant investment in conservation over the 315 last few decades (United States, Canada, Sweden). Our results are consistent with other functional work in 316 these regions, showing increases in species richness and functional diversity for North American breeding 317 birds over the last few decades after a period of decline (61), and loss of common, functionally general species 318 even as rare species are increasing in North America and Europe (62–64). 319

The final group exhibits decreasing functional evenness. These communities are of particular concern not just because of the role evenness plays in maintaining functionality, but because of increasing evidence evenness is more sensitive to environmental change than species richness (54). Formal tests of evenness changes as an early warning signal of more catastrophic shifts in functional diversity will be critical next step for understanding the full implication of evenness loss for ecosystem processes.

While the majority of studies fell into one of the groups discussed in detail above, 25% of the studies exhibited some different combination of change in metrics, underlining the vast heterogeneity of realized change scenarios. We have an indication of the ecological characteristics most likely to lead to some of the change types (e.g. temperate bird communities are gaining species and functional richness), but most types of change are exhibited across many different kinds of communities. Identifying key factors mediating the kind of biodiversity change a community experiences is critical for identifying areas of conservation concern and extrapolating results to areas where functional trait data may not be available. While it is tempting to draw a one to one line between the degree of human impact and loss of functional integrity (in the form of functional redundancy and richness), that relationship is not borne out by our rough metric of human impact (protection status) or previous taxa-specific or single community work, which is largely mixed (26, 65–67).

# 4.0.3 Areas of incongruence

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The addition of functional trait illuminated a few key areas where a synthesis approach is incongruous with system-specific studies or expectations based on anthropegenic impacts. For example, we found no evidence of general trends in CWM body mass or for studies aggregated by their characteristics despite predictions that mean body mass is decreasing as a result of climate change impacts and megafaunal loss (68). This phenomenon has also been well documented empirically and experimentally in multiple taxa (69–72). Still, climate change impacts are predicted to be most extreme for ectotherms and impact intraspecific traits first before species are lost, neither of which are represented by our data. Further, many of the studies in our dataset draw from areas that may have experienced significant loss of large-bodied species before the observation window, with contemporary loss rates slowing (73). Trends could be significantly different for the same time periods in regions of sub-Saharan Africa, for example, which has poor representation in our dataset but where megafauna exist on the landscape and are increasingly threatened (74).

Results for protected areas were also surprising given the hope that protection insulates communities from functional degradation. The only difference we found between protected and unprotected areas was significant turnover occurring outside protected areas and no significant turnover inside protected areas. While this is an indicator things are generally more static within protect areas, protection has no bearing on whether not there is change in the functional space and the nature of that change. Looking at individual studies, there is a mix of both losses and gains in almost all functional diversity and composition metrics across communities found in protected areas.

# 354 4.1 Policy Implications

While we found no over all trends in functional metrics, our results should not be interpreted as an indication that the ongoing biodiversity crisis is less severe than previously described, or that there is no concern for functional change as a result of anthropogenic impact. In fact, study-level trends indicate quite the opposite, that functional shifts with negative or yet unknown implications for ecosystem processes may be going undetected by common species-based approaches. For example, loss of evenness in communities with constant species richness may be an first sign of a community being impacted by environmental change, with negative implications for stability and function.

One of the biggest threats to biodiversity is the wholesale conversion of natural areas to urban or humandominated landscapes (75). Typical long term monitoring such as those included in our study stops before this conversion occurs, leaving the resultant precipitous declines in biodiversity unrecorded (10). This is a known issue with the culture of long term monitoring, and our results should not be removed from that context. Rather, this studies captures communities that are likely experiencing a degree of human intervention, but are still largely nature-dominated.

# 68 4.2 Future Work

The addition of functional trait data to the biodiversity change conversation is yet another illustration of 369 how critical context is for understanding ecological patterns (76, 77). Here we assessed how key community 370 characteristics such as biome, realm, taxa, and protection status may partition variation in the functional 371 trends exhibited and found that none of those characteristics seem to make the picture of change clearer. 372 Further work linking specific ecological contexts to types of functional change will be critical for identifying 373 new areas of concern, especially when those communities may not otherwise be showing significant changes in 374 species richness. The identification of contexts where functional change is most likely occurring will be a 375 significant asset in directing the future collection of trait data, a main barrier for taking a functional approach 376 to biodiversity change. 377

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## 383 References

- Barnosky AD, et al. (2011) Has the Earth's sixth mass extinction already arrived? Nature 471(7336):51–57.
- Sully S, Burkepile DE, Donovan MK, Hodgson G, van Woesik R (2019) A global analysis of coral bleaching over the past two decades. *Nature Communications* 10(1):1264.
- 388 3. Brown JH, Ernest SKM, Parody JM, Haskell JP (2001) Regulation of diversity: Maintenance of species richness in changing environments. *Oecologia* 126(3):321–332.
- Dornelas M, et al. (2014) Assemblage Time Series Reveal Biodiversity Change but Not Systematic Loss. Science 344(6181):296–299.
- Vellend M, et al. (2013) Global meta-analysis reveals no net change in local-scale plant biodiversity over time. *Proceedings of the National Academy of Sciences* 110(48):19456–19459.
- Vellend M, et al. (2017) Estimates of local biodiversity change over time stand up to scrutiny. Ecology 98(2):583–590.
- <sup>396</sup> 7. Brose U, Hillebrand H (2016) Biodiversity and ecosystem functioning in dynamic landscapes. *Philosophical Transactions of the Royal Society B: Biological Sciences* 371(1694):20150267.
- Gotelli NJ, et al. (2017) Community-level regulation of temporal trends in biodiversity. Science Advances 3(7). doi:10.1126/sciadv.1700315.
- 400 9. Li D, et al. (2020) Changes in taxonomic and phylogenetic diversity in the anthropocene. *Proceedings* of the Royal Society B: Biological Sciences 287(1929):20200777.

402 10. Cardinale B (2014) Overlooked local biodiversity loss. Science 344(6188):1098–1098.

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- 404 11. Cardinale BJ, Gonzalez A, Allington GRH, Loreau M (2018) Is local biodiversity declining or not? A summary of the debate over analysis of species richness time trends. *Biological Conservation*. doi:10.1016/j.biocon.2017.12.021.
- Gonzalez A, et al. (2016) Estimating local biodiversity change: a critique of papers claiming no net loss of local diversity. Ecology 97(8):1949–1960.
- Dornelas M, et al. (2023) Looking back on biodiversity change: Lessons for the road ahead. *Philosophical Transactions of the Royal Society B: Biological Sciences* 378(1881):20220199.
- Primack RB, et al. (2018) Biodiversity gains? The debate on changes in local- vs global-scale species richness. *Biological Conservation* 219:A1–A3.
- Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Functional Ecology 16(5):545–556.
- Mcgill B, Enquist B, Weiher E, Westoby M (2006) Rebuilding community ecology from functional traits. Trends in Ecology & Evolution 21(4):178–185.
- Suding KN, et al. (2008) Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. Global Change Biology 14(5):1125–1140.
- 18. Cardinale BJ, et al. (2012) Biodiversity loss and its impact on humanity. *Nature* 486(7401):59–67.
- 19. Dirzo R, et al. (2014) Defaunation in the Anthropocene. *Science* 345(6195):401–406.
- Young HS, McCauley DJ, Galetti M, Dirzo R (2016) Patterns, causes, and consequences of anthropocene defaunation. Annual Review of Ecology, Evolution, and Systematics 47(1):333–358.
- 21. Diáz S, Cabido M (2001) Vive la différence: Plant functional diversity matters to ecosystem processes.

  Trends in Ecology & Evolution 16(11):646–655.
- Petchey OL, Gaston KJ (2009) Effects on ecosystem resilience of biodiversity, extinctions, and the structure of regional species pools. *Theoretical Ecology* 2(3):177–187.
- Gallagher RV, Hughes L, Leishman MR (2013) Species loss and gain in communities under future climate change: consequences for functional diversity. *Ecography* 36(5):531–540.
- Petchey OL, Gaston KJ (2002) Extinction and the loss of functional diversity. Proceedings of the Royal Society of London Series B: Biological Sciences 269(1501):1721–1727.
- Pimiento C, et al. (2020) Functional diversity of marine megafauna in the Anthropocene. Science  $Advances\ 6(16)$ :eaay7650.
- Flynn DFB, et al. (2009) Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters* 12(1):22-33.
- Edwards FA, Edwards DP, Hamer KC, Davies RG (2013) Impacts of logging and conversion of rainforest to oil palm on the functional diversity of birds in Sundaland. *Ibis* 155(2):313–326.
- Larsen S, Chase JM, Durance I, Ormerod SJ (2018) Lifting the veil: richness measurements fail to detect systematic biodiversity change over three decades. *Ecology* 99(6):1316–1326.
- Matuoka MA, Benchimol M, Almeida-Rocha JM de, Morante-Filho JC (2020) Effects of anthropogenic disturbances on bird functional diversity: A global meta-analysis. *Ecological Indicators* 116:106471.
- Jackson ST, Blois JL (2015) Community ecology in a changing environment: Perspectives from the Quaternary. *Proceedings of the National Academy of Sciences* 112(16):4915–4921.
- Dornelas M, et al. (2018) BioTIME: A database of biodiversity time series for the Anthropocene. Global Ecology and Biogeography 27(7):760–786.
- Pimiento C, et al. (2017) The Pliocene marine megafauna extinction and its impact on functional diversity. Nature Ecology & Evolution 1(8):1100–1106.
- Hedberg CP, Lyons SK, Smith FA (2022) The hidden legacy of megafaunal extinction: Loss of functional diversity and resilience over the Late Quaternary at Hall's Cave. Global Ecology and Biogeography 31(2):294–307.

- Trindade-Santos I, Moyes F, Magurran AE (2020) Global change in the functional diversity of marine fisheries exploitation over the past 65 years. *Proceedings of the Royal Society B: Biological Sciences* 287(1933):20200889.
- 452 35. FitzJohn RG, et al. (2014) How much of the world is woody? Journal of Ecology 102(5):1266–1272.

453

473

- Wilman H, et al. (2014) EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals: *Ecological Archives* E095-178. *Ecology* 95(7):2027–2027.
- Blowes SA, et al. (2019) The geography of biodiversity change in marine and terrestrial assemblages. Science 366(6463):339–345.
- Norman KEA, Chamberlain S, Boettiger C (2020) taxadb: A high-performance local taxonomic database interface. *Methods in Ecology and Evolution* 11(9):1153–1159.
- R Core Team (2021) R: A language and environment for statistical computing (R Foundation for Statistical Computing, Vienna, Austria) Available at: https://www.R-project.org/.
- Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91(1):299–305.
- Mason NWH, Mouillot D, Lee WG, Wilson JB, Setälä H (2005) Functional richness, functional evenness and functional divergence: The primary components of functional diversity. *Oikos* 111(1):112–118.
- Hillebrand H, Matthiessen B (2009) Biodiversity in a complex world: consolidation and progress in functional biodiversity research: Consolidation and progress in BDEF research. *Ecology Letters* 12(12):1405–1419.
- 468 43. Leps J, Bello F, Lavorel S, Berman S (2006) Quantifying and interpreting functional diversity of natural communities: Practical considerations matter. *Preslia* 78:481–501.
- 470 44. Schleuter D, Daufresne M, Massol F, Argillier C (2010) A user's guide to functional diversity indices.

  Ecological Monographs 80(3):469–484.
- 45. Blonder B (2018) Hypervolume concepts in niche- and trait-based ecology. *Ecography* 41(9):1441–1455.
- Swenson NG, et al. (2012) The biogeography and filtering of woody plant functional diversity in North and South America. Global Ecology and Biogeography 21(8):798–808.
- 476 47. Lenth RV (2022) Emmeans: Estimated marginal means, aka least-squares means Available at: https://github.com/rvlenth/emmeans.
- 48. Bates D, Mächler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using **lme4**.

  Journal of Statistical Software 67(1). doi:10.18637/jss.v067.i01.
- 49. Kuznetsova A, Brockhoff PB, Christensen RHB (2017) lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software* 82(13):126.
- R Core Team (2023) R: A language and environment for statistical computing (R Foundation for Statistical Computing, Vienna, Austria) Available at: https://www.R-project.org/.
- Brodie JF, Williams S, Garner B (2021) The decline of mammal functional and evolutionary diversity worldwide. *Proceedings of the National Academy of Sciences* 118(3). doi:10.1073/pnas.1921849118.
- Cox DTC, Gardner AS, Gaston KJ (2022) Global and regional erosion of mammalian functional diversity across the diel cycle. *Science Advances* 8(32):eabn6008.
- Li X, et al. (2022) Functional diversity loss and change in nocturnal behavior of mammals under anthropogenic disturbance. *Conservation Biology* 36(3):e13839.
- Filstrup CT, King KBS, McCullough IM (2019) Evenness effects mask richness effects on ecosystem functioning at macro-scales in lakes. *Ecology Letters* 22(12):2120–2129.
- Hillebrand H, Bennett DM, Cadotte MW (2008) Consequences of Dominance: A Review of Evenness Effects on Local and Regional Ecosystem Processes. *Ecology* 89(6):1510–1520.
- bagousse-Pinguet YL, et al. (2019) Phylogenetic, functional, and taxonomic richness have both positive and negative effects on ecosystem multifunctionality. *Proceedings of the National Academy of Sciences* 116(17):8419–8424.
- Spatz DR, et al. (2023) Tracking the global application of conservation translocation and social attraction to reverse seabird declines. *Proceedings of the National Academy of Sciences* 120(16):e2214574120.

- Reich PB, et al. (2012) Impacts of biodiversity loss escalate through time as redundancy fades. Science (New York, NY) 336(6081):589–592.
- 500 59. Pimiento C, et al. (2020) Selective extinction against redundant species buffers functional diversity.

  Proceedings of the Royal Society B: Biological Sciences 287(1931):20201162.
- Biggs CR, et al. (2020) Does functional redundancy affect ecological stability and resilience? A review and meta-analysis.  $Ecosphere\ 11(7)$ :e03184.
- Jarzyna MA, Jetz W (2016) A near half-century of temporal change in different facets of avian diversity. Global Change Biology 23(8):2999–3011.
- Inger R, et al. (2015) Common European birds are declining rapidly while less abundant species' numbers are rising. *Ecology Letters* 18(1):28–36.
- Rosenberg KV, et al. (2019) Decline of the North American avifauna. Science. Available at: https://www.science.org/doi/abs/10.1126/science.aaw1313.
- Schipper AM, et al. (2016) Contrasting changes in the abundance and diversity of North American bird assemblages from 1971 to 2010. *Global Change Biology* 22(12):3948–3959.
- 512 65. Luck GW, Carter A, Smallbone L (2013) Changes in Bird Functional Diversity across Multiple Land Uses: Interpretations of Functional Redundancy Depend on Functional Group Identity. *PLOS ONE* 8(5):e63671.
- Magioli M, et al. (2021) Land-use changes lead to functional loss of terrestrial mammals in a Neotropical rainforest. *Perspectives in Ecology and Conservation* 19(2):161–170.
- Tinoco BA, Santillán VE, Graham CH (2018) Land use change has stronger effects on functional diversity than taxonomic diversity in tropical Andean hummingbirds. *Ecology and Evolution* 8(6):3478–3490.
- 518 68. Sheridan JA, Bickford D (2011) Shrinking body size as an ecological response to climate change.

  Nature Climate Change 1(8):401–406.
- <sup>520</sup> 69. Caruso NM, Sears MW, Adams DC, Lips KR (2014) Widespread rapid reductions in body size of adult salamanders in response to climate change. *Global Change Biology* 20(6):1751–1759.
- Forster J, Hirst AG, Atkinson D (2012) Warming-induced reductions in body size are greater in aquatic than terrestrial species. *Proceedings of the National Academy of Sciences* 109(47):19310–19314.
- 71. Huss M, Lindmark M, Jacobson P, van Dorst RM, Gårdmark A (2019) Experimental evidence of gradual size-dependent shifts in body size and growth of fish in response to warming. *Global Change Biology* 25(7):2285–2295.
- Tseng M, et al. (2018) Decreases in beetle body size linked to climate change and warming temperatures.  $Journal\ of\ Animal\ Ecology\ 87(3):647-659.$
- Fritz SA, Bininda-Emonds ORP, Purvis A (2009) Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. *Ecology Letters* 12(6):538–549.
- 74. Ripple WJ, et al. (2015) Collapse of the world's largest herbivores. Science Advances 1(4):e1400103.
- Tilman D, et al. (2017) Future threats to biodiversity and pathways to their prevention. Nature 546(7656):73-81.
- 76. Catford JA, Wilson JRU, Pyšek P, Hulme PE, Duncan RP (2022) Addressing context dependence in ecology. Trends in Ecology & Evolution 37(2):158–170.
- 536 77. Spake R, et al. (2023) Understanding 'it depends' in ecology: a guide to hypothesising, visualising and interpreting statistical interactions. *Biological Reviews* 98(4):983–1002.
- Pardieck KL, David ZJ, Lutmerding M, Aponte V, Hudson M-AR (2020) North american breeding bird survey dataset 1966 2019, version 2019.0. doi:10.5066/P9J6QUF6.
- 79. PIROP northwest atlantic 1965–1992 OBIS SEAMAP Available at: http://www.iobis.org/mapper/ 70. PIROP northwest atlantic 1965–1992 - OBIS SEAMAP Available at: http://www.iobis.org/mapper/
- 542 80. Silva FR da Brazil dataset 1.

543

Scott D, Metts B, Lance S The rainbow bay long-term study. Available at: http://srelherp.uga.edu/projects/rbay.htm.

- Rossa-Feres D de C (1997) Community ecology of anura amphibia at northwest region of sao paulo state, brazil: Microhabitat, seasonality, diet and multidimensional niche. PhD thesis.
- Bakker C, Herman PMJ (1990) Phytoplankton in the oosterschelde before, during and after the storm-surge barrier (1982–1990). Available at: http://www.iobis.org/mapper/?dataset=505.
- 550 84. Berezovikov, N.N. (2004) The birds of settlements in markakol depression (southern altai). (249):3–15.
- Enemar A, Sjöstrand B, Andersson G, Von Proschwitz T (2004) The 37-year dynamics of a subalpine passerine bird community, with special emphasis on the influence of environmental temperature and epirrita autumnata cycles. *Ornis Svecica* 14(3):63–106.
- $^{554}$  86. Gido K (2019) CFP01 Fish population on selected watersheds at Konza Prairie. doi:10.6073/PASTA/BE5AD393AF83F9602AAE96423A280875.
- Hogstad O (1993) Structure and dynamics of a passerine bird community in a spruce-dominated boreal forest. A 12-year study. *Annales Zoologici Fennici* 30(1):43–54.
- Holmes RT, Sherry TW, Sturges FW (1986) Bird Community Dynamics in a Temperate Deciduous Forest: Long-Term Trends at Hubbard Brook. *Ecological Monographs* 56(3):201–220.
- Jahncke J, Rintoul C (2006) CalCOFI and NMFS seabird and marine mammal observation data, 1987–2006. Available at: http://www.iobis.org.
- 562 90. Krivenko, V.G. (1991) Waterfowl and their protection.

563

573

587

- Melnikov, Y.I., Melnikova, N., Pronkevich, V.V. (2000) Migration of birds of prey in the mouth of the river irkut. (108):3–17.
- Monitoring Site 1000 Project, Biodiversity Center, Ministry of Environment of Japan (2013) Monitoring site 1000 shorebird survey. Available at: http://www.biodic.go.jp/moni1000/findings/data/index.html.
- Monitoring Site 1000 Project, Biodiversity Center, Ministry of Environment of Japan (2014) Monitoring site 1000 village survey bird survey data (2005-2012). Available at: http://www.biodic.go.jp/moni1000/findings/data/index.html).
- Monitoring site 1000 village survey medium and large mammal survey data (2006-2012) (2014) Available at: http://www.biodic.go.jp/moni1000/findings/data/index.html.
- 572 95. Preston FW (1960) Time and space and the variation of species. Ecology 41(4):612–627.
- Svensson S (2006) Species composition and population fluctuations of alpine bird communities during 38 years in the scandinavian mountain range. *Ornis Svecica* 16:183–210.
- 576 97. Svensson S, Thorner AM, Nyholm NEI (2010) Species trends, turnover and composition of a woodland bird community in southern sweden during a period of fifty-seven years. Ornis Svecica 20(1).

  577 doi:10.34080/os.v20.22641.
- Thorn S, et al. (2016) Changes in the dominant assembly mechanism drive species loss caused by declining resources. *Ecology Letters* 19(2):163–170.
- USFS Landbird monitoring program (UMT-LBMP). Available at: http://www.avianknowledge.net/.
- Vermont Center For Ecostudies, Lambert JD, Hart J (2015) Mountain Birdwatch 1.0. doi:10.5063/F1DN430G.
- $^{584}$  101. Vickery WL, Nudds TD (1984) Detection of Density-Dependent Effects in Annual Duck Censuses.  $Ecology\ 65(1):96-104.$
- <sup>586</sup> 102. Waide R (2017) Bird abundance point counts. doi:10.6073/PASTA/91E6302E743BAC1E3E32781B869CE3D9.
- $^{588}$  103. Williamson M (1983) The land-bird community of skokholm: Ordination and turnover. Oikos 41(3):378–384.
- Zakharov, V.D. (1998) Biodiversity of bird population of terrestrial habitats in southern ural. Miass: IGZ. Available at: http://ashipunov.info/shipunov/school/books/zakharov1998\_biorazn\_nasel\_ptits\_mazemn\_mestoob\_juzhn\_urala.pdf.
- MEDITS seabird surveys 1999 / 2000 / 2002 (2011) Available at: http://www.emodnet-biology.eu/component/imis/?module=dataset&dasid=1979.

- Animal demography unit coordinated waterbird counts (CWAC) AfrOBIS Available at: http://www.iobis.org/.
- Baltic seabirds transect surveys Available at: http://www.emodnet-biology.eu/component/imis/ 7module=dataset&dasid=1971.
- Thorn S, et al. (2016) Response of bird assemblages to windstorm and salvage logging Insights from analyses of functional guild and indicator species. *Ecological Indicators* 65:142–148.
- Ernest SKM, Valone TJ, Brown JH (2009) Long-term monitoring and experimental manipulation of a Chihuahuan Desert ecosystem near Portal, Arizona, USA: Ecological Archives E090-118. Ecology 90(6):1708–1708.
- Friggens M (2008) Sevilleta LTER small mammal population data. Available at: http://sev.lternet.edu/data/sev-8.
- Jalilov, A. B., Andreychev, A. V., Kuznetsov, V. A. (2014) Monitoring and conservation of medium and large mammals in chamzinsky district of the republic of mordovia.
- 606 112. Kartzinel TR, et al. (2014) Plant and small-mammal responses to large-herbivore exclusion in an African savanna: five years of the UHURU experiment: *Ecological Archives* E095-064. *Ecology* 95(3):787–787.
- 608 113. Kaufman D (2019) CSM01 Seasonal Summary of Numbers of Small Mammals on 14 LTER Traplines in Prairie Habitats at Konza Prairie. doi:10.6073/PASTA/9735A16A0018D85FF5EFB8B74FD100F4.
- $^{610}$  114. Krefting LW, Ahlgren CE (1974) Small Mammals and Vegetation Changes After Fire in a Mixed Conifer-Hardwood Forest.  $Ecology\ 55(6):1391-1398.$
- Lightfoot D, Schooley RL SMES rodent trapping data, small mammal exclosure study. Available at:
  http://jornada.nmsu.edu/sites/jornada.nmsu.edu/files/data\_files/JornadaStudy\_086\_smes\_rodent\_trapping\_data\_0
  accessed 2016.
- Malyshev, Y. S. (2011) On the diagnostic techniques of ranks of the number dynamics cycles of small mammals. 1(6):92–106.
- Meyer CFJ, Kalko EKV (2008) Assemblage-level responses of phyllostomid bats to tropical forest fragmentation: land-bridge islands as a model system. *Journal of Biogeography* 35(9):1711–1726.
- Nedosekin, V. Y. (2015) Long-term dynamics of the population and the quantity of small mammals under conditions of the reserve "galichya gora".
- Prins HHT, Douglas-Hamilton I (1990) Stability in a multi-species assemblage of large herbivores in East Africa. Oecologia~83(3):392-400.
- Rocha R, et al. (2017) Consequences of a large-scale fragmentation experiment for Neotropical bats: disentangling the relative importance of local and landscape-scale effects. *Landscape Ecology* 32(1):31–45.
- Stapp P (2014) SGS-LTER long-term monitoring project: Small mammals on trapping webs on the central plains experimental range, nunn, colorado, USA 1994 -2006, ARS study number 118.
   doi:10.6073/PASTA/2E311B4E40FEA38E573890F473807BA9.
- Bahamas marine mammal research organisation opportunistic sightings OBIS SEAMAP Available at: http://www.iobis.org.
- POPA cetacean, seabird, and sea turtle sightings in the azores area 1998–2009 OBIS SEAMAP Available at: http://www.iobis.org/mapper/?dataset=4257.